

Canis rufus. By John L. Paradiso and Ronald M. Nowak.

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Canis rufus Audubon and Bachman, 1851 Red Wolf

Lupus niger Bartram, 1791:199. Type locality, Alachua Savanna (now Payne's Prairie), Alachua County, Florida. The International Commission on Zoological Nomenclature in Opinion 447, published 29 January 1957, placed Bartram (1791) on its official Index of Rejected and Invalid Works in Zoological Nomenclature (see Nowak, 1967).

Canis lupus var. *rufus* Audubon and Bachman, 1851, 2:240. Type locality designated by Goldman (1937:45) as 15 miles west of Austin, Texas.

Canis rufus: Bailey, 1905:174, first use of name combination.

CONTEXT AND CONTENT. Order Carnivora, Family Canidae, Subfamily Caninae. Three subspecies are currently recognized (Goldman, 1937:45) as follows:

C. r. floridanus Miller, 1912:95. Type from Horse Landing, St. Johns River, about 12 miles south of Palatka, Putnam County, Florida.

C. r. gregoryi Goldman, 1937:44. Type from Macks Bayou, 3 miles east of Tensas River, 18 miles southwest of Tallulah, Madison Parish, Louisiana.

C. r. rufus Audubon and Bachman, 1851, Vol. 2:240, see above.

DIAGNOSIS. As noted by Goldman (Young and Goldman, 1944:400), there is such a great degree of individual, geographic, sexual, and age variation within each species of North American *Canis*, and such wide specific overlap in most characters, that much of the following diagnosis is necessarily general and qualitative in nature. Positive identification of specimens often requires comparison with large series. Measurements and ratios in this diagnosis pertain to specimens in the United States National Museum.

C. rufus is highly variable in all characters; the following, however, are the most diagnostic. Skull narrow and elongated with long, slender rostrum, and flat frontal region; postorbital constriction relatively narrow and elongated; braincase relatively small; sagittal crest usually well-developed (see figure 1). Canine teeth long and slender, generally extending below the level of a line drawn across the anterior mental foramina when the jaws are closed; pronounced deuterocone present on P4 (capital initials indicate upper teeth); metaconule well-developed on M1; pronounced cingulum on upper molar teeth; M2 large in proportion to size of skull (zygomatic breadth averages 11.3 times greatest transverse diameter of M2 in 158 specimens). Greatest length of skull for adult specimens from Louisiana, Arkansas, and Missouri, collected prior to 1930, ranges from 217.5 to 261.0 mm for 74 males, and from 209.9 to 247.0 mm for 69 females.

Compared with *C. latrans*, *rufus* is always larger, both externally and cranially when specimens of only one sex are compared (the greatest length of skull of *latrans* ranges from 173.4 to 215.8 mm for 176 males and from 171.6 to 204.5 for 115 females). The sagittal crest in *rufus* invariably exhibits more pronounced development; the postorbital constriction is relatively narrower and more elongated, and the braincase relatively smaller and more heavily ossified. The M2 is smaller in proportion to size of skull than in *latrans* (zygomatic breadth averages 11.9 times greatest transverse diameter of M2 measured diagonally in 330 adult specimens of *latrans* collected throughout the range of the species). In all other cranial and dental details, *rufus* and *latrans* show a strong resemblance to each other.

Canis rufus resembles *C. lupus* in size (72 male *lupus* range from 230.7 to 286.9 mm, and 50 females from 224.0 to 277.5 mm in greatest length of skull) but differs as follows: the skull is more slender and less massive (although in greatest length a *rufus* skull may be longer); rostrum longer and narrower; canine teeth longer (in *lupus* they do not extend below a line drawn across the anterior mental foramina when the jaws are closed); pronounced deuterocone present on

P4; metaconule well marked on M1; cingulum on upper molars. The M2 is larger in proportion to size of skull than in *lupus* (zygomatic breadth averages 9.8 times greatest transverse diameter of M2 measured diagonally in 184 adult specimens of *lupus* collected throughout the range of the species).

Canis rufus usually can be differentiated from *C. familiaris* by a combination of pelage, cranial, and dental characters. In *rufus* the teeth (particularly P1, M1, and M2) are generally larger; canine teeth longer and more slender proportionally; rostrum relatively longer and more slender, and frontal region flatter. The domestic dog is such a variable animal, however, that some species can closely resemble any of the wild species of North American *Canis*.

Other differences and similarities between *rufus*, *latrans*, *lupus*, and *familiaris*, are discussed by Goldman (Young and Goldman, 1944) and Lawrence and Bossert (1967).

GENERAL CHARACTERS. Doglike in general form, with size averaging intermediate between *lupus* and *latrans*, although some large specimens of *rufus* overlap smaller specimens of *lupus* in measurements and weight. Weights and measurements given in this section are based on specimens and records in the United States National Museum, or upon reports by Bureau of Sport Fisheries and Wildlife biologists in the field.

Total length of *rufus* ranges from about 1355 to 1650 mm (*latrans* about 1050 to 1320 mm, and *lupus* about 1370 to 2050 mm). Recently collected specimens from Chambers County, Texas, measured between 1359 and 1493 mm in total length. Adult *rufus* collected in Arkansas prior to 1930 weighed as follows (averages followed by extremes): 23 males, 60.9, 45 to 90 lbs (21 to 41 kg); 34 females, 47.6, 36 to 65 lbs (16 to 29 kg). Six specimens weighed recently (1970) by Bureau of Sport Fisheries and Wildlife field agents in Chambers County, Texas, were between 45 and 62 lbs, and averaged about 52 lbs (24 kg). A recently collected (1970) male and female from Galveston County, Texas, weighed 50 lbs and 45 lbs, respectively, and the largest animal from Liberty County was 54 lbs. One recently trapped (1970) Chambers County male had a shoulder height of 28 inches (0.7 m). Young and Goldman (1944:69) stated that the weight of fully mature *lupus* is between 60 and 175 lbs (27 and 77 kg), whereas *latrans* generally ranges from 18 to 30 lbs (8 to 14 kg) (Young and Jackson, 1951:48).

A detailed description of the coloration of *rufus* was given by Goldman (Young and Goldman, 1944:480). The most common color phase in a large series of *rufus* skins (specimens collected prior to 1930 in Louisiana, Texas, Oklahoma, Arkansas and Missouri) appears more reddish and more sparsely haired than series of *latrans* and *lupus* in comparable pelage. Nevertheless, individual skins of all three, and some of *familiaris* as well, can be found that are virtually indistinguishable from one another; coloration does not appear to be a diagnostic character in North American *Canis*. Both *rufus* and *lupus* often occur in a black color phase, but according to Young (Young and Jackson, 1951:52), black coloration is extremely rare among coyotes.

Young (1946:36) stated with regard to *rufus*: "It is rather greyhound-like in appearance, with long, somewhat spindly legs." Although there are actually no comparative measurements as yet to confirm this, long legs in *rufus* have been commented upon by several field biologists of the Bureau of Sport Fisheries and Wildlife who have worked with the species recently on the Texas Coast. Glynn A. Riley, Jr., Principal District Field Assistant for the Division of Wildlife Services, Bureau of Sport Fisheries and Wildlife, Liberty, Texas, reported (September 1970) that the legs of *rufus* are strikingly long and slender, giving the animal almost the appearance of "being on stilts." Riley also reported that the ears of *rufus* are far larger in proportion to the size of the head than are the ears of the *latrans* and *lupus* with which he has worked.

DISTRIBUTION. Probably the original range of *rufus* coincided well with the Louisianian, Carolinian, and Texan

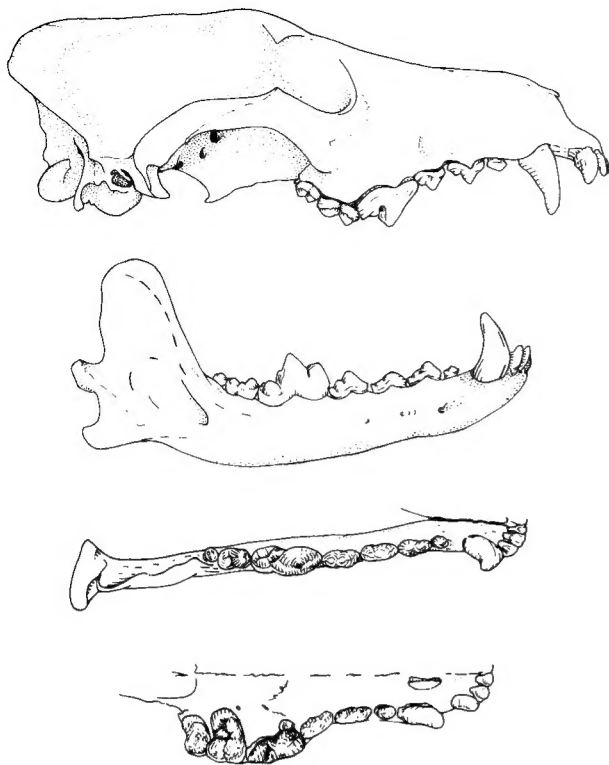


FIGURE 1. Skull of *Canis rufus* from Cook Station, Crawford County, Missouri, collected on 2 April 1924 (USNM 244489). Drawings by Mrs. Wilma Martin.

mammal provinces of Hagmeier (1966), but the species was extirpated at such an early date in the eastern United States that it is impossible to be certain. Specimens confirm that it formerly occurred in Florida, Alabama, Mississippi, Louisiana, Arkansas, southern Missouri, southern Indiana, eastern Oklahoma, and eastern Texas (see figure 2). Goldman (Young and Goldman, 1944:486) assigned a specimen from Warsaw, Hancock County, Illinois, and another supposedly from Wabash, Wabash County, Indiana, to *rufus* and thus placed the limits of distribution of the species somewhat too far north. The specimen from Illinois, in the collection of the American Museum of Natural History, was received from C. K. Worthen, an animal dealer whose home was in Hancock County, Illinois. Apparently the specimen was a captive animal, and it is impossible to be certain of the locality data (E. Raymond Hall, personal communication). The faded label of the specimen from Indiana shows that it was actually taken in the Wabash River area of southern Indiana.

In the western part of the range of the species, Goldman (Young and Goldman, 1944:489) listed a specimen of *rufus* from Sheffield (22 miles north), Pecos County, Texas. This specimen is in the United States National Museum collection, and is actually a coyote, *C. latrans*. There is no evidence that *rufus* ever occurred farther west in Texas than the Edwards Plateau.

C. rufus has been exterminated over most of its former range. At the present time it is known to occur in its pure form (hybridization with *latrans* is discussed under section on Genetics) only in the coastal prairies and marshes of the Gulf Coast counties of southeastern Texas and adjacent Louisiana (Paradiso, 1965; Nowak, 1970, 1972). Specimens have been obtained since 1960 and deposited in the United States National Museum from Brazoria (east of the Brazos River), Chambers, Liberty, Harris and Jefferson counties, Texas. For information on the occurrence of *rufus* in Louisiana and Arkansas see Nowak, 1967, 1970 and Pimlott and Joslin, 1968.

FOSSIL RECORD. No fossils have been assigned to *C. rufus* and there have been few attempts at direct comparison of the modern red wolf to Pleistocene specimens. One of these few was by Gazin (1942) who, in describing *Canis edwardii* from the early Pleistocene of Arizona, stated (p. 501): "The skull and jaw of *C. edwardii* . . . are about intermediate in

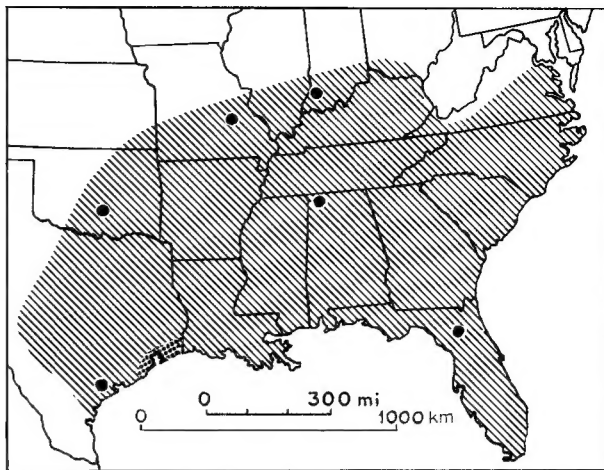


FIGURE 2. Map illustrating distribution of *Canis rufus*. The shaded portion shows the probable distribution prior to 1600. The dots represent the most marginal specimens (in museum collections) that can definitely be assigned to pure *C. rufus*. The stippling depicts the area in southeastern Texas where pure populations of *C. rufus* now occur as indicated by specimens. The species also probably now exists in southern Louisiana.

size between those of a gray wolf, and of a coyote, about equalling specimens of the red wolf, *Canis rufus* from Missouri and Arkansas. . . . The teeth are comparable to those in the red wolf and resemble them in structure more closely than they do any other species of canids." He did not, however, suggest phylogenetic affinity between the two species, and considering the wide variation that *Canis* has always shown, it cannot be established that *edwardii* definitely represents any continuum with modern *rufus*.

Another reference to a fossil in relation to modern *rufus* involves *Canis armbrusteri* Gidley, from Pleistocene deposits in Cumberland Cave, Maryland. Goldman (Young and Goldman, 1944:399), in discussing *armbrusteri*, stated only that it "appears to have been allied to the red wolf, *Canis niger*. . . ."

Hibbard (1955:52) reported a right ramus of a small wolf in the late Pleistocene Upper Becerra Formation, Valley of Tequiquiac, Mexico. He noted: "The specimen is smaller than *Canis lupus* Linnaeus and appears closely related to *Canis niger* Bartram. But the true relationship will not be known until the upper dentition is found."

Nowak (1970:84) considered the possibility that the progenitor of *C. rufus* was closely related to *C. latrans*, but had become isolated in the southeastern United States by Pleistocene glaciation. He reported: "A late Pleistocene (Wisconsin) fossil from Alachua County, Florida, appears to represent an animal transitional between a coyotelike ancestor and the modern red wolf."

FORM. Atkins and Dillon (1971) compared the gross morphology of the cerebella of a number of species of the genus *Canis*, including *rufus*, and found that the cerebella indicated a division of the genus into two groups: a *rufus-lupus* group and a *latrans-familiaris*-jackal group. However, *rufus* displays numerous and obvious characteristics that distinguish it from *lupus*.

Although Atkins and Dillon believed that the cerebellum of *rufus* indicates that its closest affinities are with *lupus*, they found that the *rufus* cerebellum differs from that of all species of *Canis* examined in several important traits, and resembles in some characters the cerebellum of the foxes they studied (*Alopex lagopus*, *Urocyon cinereoargenteus*, *Vulpes chama*, *V. velox*, and both European and American *V. vulpes*). They considered the cerebella of these foxes to be more primitive in structure than those in *Canis*, and suggested that a retention of some foxlike characters in the *rufus* cerebellum may indicate that *rufus* is nearer to the common ancestral stock of *Canis* than are the other species of modern *Canis* they examined.

ONTOGENY AND REPRODUCTION. Nothing has been published on reproduction and development in *rufus*. Data in the files of the Bureau of Sport Fisheries and Wildlife (pertaining to specimens taken prior to 1930) reveal the following. In Arkansas, females with embryos were trapped

between 28 February and 10 May; females with suckling young from 20 April to 6 June. Pregnant females were taken in Oklahoma from 14 March to 16 April. In Texas, females with unborn young were trapped from 7 March to 16 May; females with suckling young from 5 April to 3 June. Thus, it appears that copulation in this species occurs from late December or early January to late February or early March, and that young are born in April, May, and perhaps early June. Twenty-nine pregnant females from Arkansas, Oklahoma, and Texas had embryos varying in number from two to 10, with an average of 6.62. John Steele, formerly with the Bureau of Sport Fisheries and Wildlife's Endangered Species Program for the red wolf in east Texas reported (personal communication, October 1969) that recent observations on the Gulf Coast of Texas indicate that reproductive success of *rufus* is on a low level there. Litter size averages 7, but most young die before they are six months old. No reproduction was noted in Chambers County in 1968. Steele reported that red wolves in this region copulate for the first time just before they are three years old, and whelp early in May. Older animals breed earlier and whelp in April. He also reported a gestation period of 60 to 62 days for a litter born in the zoo at Lufkin, Texas.

ECOLOGY. No comprehensive survey of the ecology of *rufus* has been made. The following sketchy information, however, is available.

The range of *C. rufus* was mostly within the humid division of the Lower Austral Life Zone, and the species apparently preferred a warm, moist, and densely vegetated habitat. The red wolf was equally at home in the virgin pine forests, bottomland hardwood forests, or coastal prairies and marshes of the southeast. The body proportions of the species may be an adaptation both for life in swamps and marshes, and for long-distance running in coastal prairies and in the original open pine forest of the southeast. The cutting over of the forests of the southeastern United States, probably contributed to the decline of *rufus* (Nowak, 1970).

Canis rufus does not appear to have been a major predator of big game. There are few records of its attacking large herbivores, such as are numerous for *lupus*. Attempts to list the food of *rufus* (Young and Goldman, 1944; Davis, 1960; Beezley, 1967) refer mostly to rabbits, rodents, and other small prey. Concerning the Louisiana red wolf, St. Amant (1959:185) stated that it is not known to what extent it preys on deer, and that the major wolf concentrations are not necessarily in the areas most densely populated by deer. Even reports such as Howell's (1921) of red wolf predation on domestic stock generally refer to small or younger animals being taken. It should not be presumed, however, that the red wolf exclusively preys on animals smaller than itself. Catesby (1743, 2:26) wrote that wolves pursued deer in the Carolinas, and Young (1946:39) noted that wild razorback hogs formed a major part of the food of the red wolves found in the Tensas River region of Louisiana. Jackson (1961) stated that groups of three or more red wolves were generally successful in attacking adult cattle on the JHK ranch in Chambers County, Texas. In general, it appears that the prey of *rufus* is intermediate in size between that of *latrans* and *lupus*.

According to John Steele (personal communication, October 1969) causes of mortality for the red wolf in the Texas Gulf Coast area include man, hookworms, distemper, and accidents. Most pups acquire hookworms and are so weakened by them that they cannot keep up with their parents. They die indirectly from hookworms, and adults have a shortened life span due to hookworms and heartworms. Most of the adults he captured during his surveys were anemic and had low level infections of one sort or another.

Man is probably the greatest enemy of *rufus*, and deliberate killing appears to be one of the major factors in the decline of the species (Nowak, 1970). All personnel of the Bureau of Sport Fisheries and Wildlife (Steele, McBride, Riley) who have recently worked with *C. rufus* in the Gulf Coast area of Texas, have commented (in personal communications) on the ease with which red wolves can be trapped or poisoned. The species resembles *latrans* in that it is able to survive in areas of relatively dense human populations—*rufus* runways have been found in Galveston County, Texas, within sight of housing developments (Riley, personal communication, September 1970)—but it does not appear to possess the cunning and caution widely attributed to *latrans*. The apparent ease of trapping *rufus*, combined with ecological

changes induced by man, appear to be the major factors in the decline of the species (McCarley, 1962; Paradiso, 1968; Nowak, 1970).

BEHAVIOR. Young (1946:36) noted the long legs and slender build of *rufus* and felt that its greyhound-like body would make it a better long distance runner than *latrans*. Riley (personal communication, September 1970) also was impressed by the long legs of *rufus* and stated that it appeared to him that the red wolf was an animal adapted for coursing in open country.

Steele (personal communication, October 1969) stated that in east Texas most *rufus* hold their tails down at a 45° angle when standing, but some animals hold it near back level. Nearly all carry it horizontally when they run. During greetings and courtship, they raise it high above their backs, perhaps to activate scent glands.

He also stated that *rufus* does not run like a dog, but has a bounding motion, somewhat like a rocking horse, pausing when the shoulders are highest. Red wolves investigate sounds and noises by standing up on their hind legs, especially in tall grass and weeds.

Steele noted that in the Texas Gulf Coast counties red wolves are most active at night, generally at the same time rabbits are feeding. Sometimes red wolves bed down at night in the middle of a herd of cattle. In daylight, they rest in weedy fields, or grass or brush pastures. From April to mid-August red wolves restrict their travels to the point that track signs all but disappear. Beginning in September, they resume travel over a hunting range. Mated pairs, sometimes with an extra male, travel together. Packs of from five to 11 animals may get together temporarily, but break up into family groups soon after exchanging greetings. Pairs travel around a range using established runways marked by scent posts and scratch marks.

Red wolves have a long smooth howl that ends on a slightly higher note. They also have a wide variety of yodeling cries that sound exactly like those of coyotes. Vernon Bailey in a 1904 special report to the U. S. Biological Survey wrote of the wolves in the Big Thicket of Hardin County, Texas: "Their voice is a compromise between that of the coyote and the lobo [*C. lupus*], or rather a deeper varied yap yap and howl of the coyote. It suggests the coyote much more than the lobo."

Steele further noted that in the Texas Gulf Coast area dens are found in hollow logs, stumps, road culverts, sand knolls, and banks of canals, ditches, and reservoirs. They are generally screened from view by berry vines, wild roses, brush piles, trees, etc.

GENETICS. Studies conducted at the M. D. Anderson Hospital and Tumor Institute, University of Texas, Houston, have demonstrated that the diploid chromosome number of a red wolf collected in 1966 in Jefferson County, Texas, was 78, and that the X chromosome only is biamed. The karyotype of this specimen is thus indistinguishable from those of *latrans*, *lupus*, and *familiaris*, and chromosomal factors would not inhibit interbreeding among these species (Frances E. Arrighi, personal communication, August 1969; and Mammalian Chromosomes Newsletter 21:159, July 1966).

Goldman (Young and Goldman, 1944:480) first noted the possibility of hybridization between *latrans* and *rufus*. He wrote: "Specimens collected in the vicinity of Llano, Tex. include typical examples of both species and individuals not sharply distinctive of either. Close approach in essential details and the apparent absence of any invariable unit character suggest the possibility of hybridism in some localities in Texas."

McCarley (1962) felt that hybridization with *latrans* was possibly one of the factors that brought about the near extermination of *rufus*. He further suggested that the entire subspecies *C. r. rufus* might be a population of natural hybrids between *C. latrans* and *C. rufus gregoryi*.

Lawrence and Bossert (1967), using a multiple character analysis, found that a small sample of *Canis* from Fallsville, Newton County, Arkansas, spanned the whole range of variation from coyote to wolf and felt that this indicated possible hybridization.

Paradiso (1968) examined a large series of *Canis* from east Texas collected after 1960, and found that they also spanned the whole range of variation from typical *latrans* to typical *rufus*, with all intermediates represented. He concluded that massive hybridization had occurred between the two species in this region.

Nowak (1970) reported that his studies with Paradiso at the United States National Museum indicated that in most areas the red wolf died out as a result of heavy hunting and trapping pressures and massive environmental changes that were unfavorable to the species. Specimens in the National collection indicated that in many areas *rufus* was replaced by pure *latrans* and there was no indication of hybridization between the two. Specimens from the Edwards Plateau of central Texas, collected around the turn of the present century, did show intermediate characters between *rufus* and *latrans*, leading Nowak to postulate that a hybrid swarm formed here. He further postulated that this hybrid swarm migrated eastward, occupying territory from which *C. rufus* had been extirpated, and today it occurs throughout most of eastern Texas and Louisiana. Specimens indicated that the upper Gulf Coast region of Texas and probably adjacent Louisiana are perhaps the only areas in which *C. rufus* continues to survive as a pure species. Nowak reported that early specimens of *C. r. rufus* in the National collection led him to believe that it was a valid subspecies of *rufus* and did not represent hybrids as suggested by McCarley (1962).

REMARKS. There are a number of differing opinions regarding the taxonomic affinities of *rufus*. Goldman (Young and Goldman, 1944) regarded *rufus* as a full species, distinct from both *latrans* and *lupus*. Paradiso (1968), struck by what he thought was massive hybridization between *rufus* and *latrans* in east Texas, suggested that the two might be conspecific. Lawrence and Bossert (1967:229) concluded from their multiple character analysis that "early populations described as *Canis niger* [= *C. rufus floridanus*] and *n. gregoryi* [= *C. rufus gregoryi*] from the southeastern wooded regions, east of the range of *Canis latrans*, are only a local form of *Canis lupus*, not a distinct species of wolf." Nowak (1970) reported trenchant differences between *rufus*, *lupus*, and *latrans*, and regarded *rufus* as a full species. Atkins and Dillon (1971) also presented evidence from brain morphology that *rufus* should stand apart as a distinct species from other North American *Canis*. Studies currently being conducted by Nowak at the University of Kansas on Pleistocene and Recent *Canis* in North America, and serological studies by Ulysses S. Seale of the University of Minnesota, may throw additional light on the relationships of *Canis rufus*.

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